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NOTES ON THE REMARKABLE KARYOLOGY OF THE PRIMITIVE ANT *NOTHOMYRMECIA MACROPS*, AND OF THE RELATED GENUS *MYRMECIA* (HYMENOPTERA: FORMICIDAE)

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INTRODUCTION

Nothomyrmecia macrops Clark (subfamily Nothomyrmecinae) is arguably the most primitive of all known ants, and study of this "living fossil" has been deemed "one of the principal challenges of modern Australian entomology" (Brown and Wilson, 1959). Its first two worker representatives were collected in southeastern Western Australia in 1932-33 (Clark, 1934), but despite much effort by many naturalists *Nothomyrmecia* was not encountered again for nearly half a century, until rediscovered in 1977 near Poochera (32°43'S; 134°50'E), South Australia (about 1000 km east of the original site) by R. W. Taylor and colleagues (Taylor, 1978). It has not been found again in Western Australia, and the known distribution at Poochera lies within a radius of only about 1 kilometre.

Reasons for this resistance to collection by *Nothomyrmecia* include its purely nocturnal above-ground worker activities, which are further restricted to relatively cold nights, its cryptic nesting habits, and probably very patchy distribution. Aspects of its anat-

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omy and behaviour (Taylor, 1978; Hölldobler and Taylor, 1983) imply that *N. macrops* could reasonably exemplify an early stage in ant evolution following the acquisition of eusociality.

Information on the chromosomes of this significant insect is important for analysis of karyotype evolution among the ants. An initial cytological check was expedited by A. D. Bishop and R. H. Crozier (Taylor, 1978). They obtained a $2n$ count of "about 92" for the worker caste, but, because of the high number and small size of the chromosomes, could not be more precise.

The authors were able recently to visit the Poochera site, to collect adequate new material, and to obtain more satisfactory chromosomal preparations.

RESULTS

The subject *Nothomyrmecia* colony (code HI89-013) was collected on 14 December, 1989. Brains from several prepupal workers (at the stage following spinning of the pupal cocoon, and immediately after release of the meconium) were prepared using the air-drying technique of Imai et al. (1977, 1988). A total of 10 well-spread metaphase figures were obtained (2 cells each from individuals nos 1 and 2; 1 from no. 5; and 5 from no. 6). All yielded $2n=94$.

Detailed analysis reveals that the diploid karyotype (Fig. 1) comprises one pair of large, and one of medium-sized, metacentrics (M), one pair of medium-sized subtelocentrics (ST), and 44 pairs of medium or small-size acrocentrics (A) or pseudo-acrocentrics (acrocentrics with extremely elongated heterochromatic short arms) (A^M) — i.e. $2K = 4M + 2ST + 88A$ or A^M . All cells examined had the same homomorphic karyotype, and no chromosomal polymorphisms were detected.

DISCUSSION

The two highest chromosome numbers previously recorded for families of the order Hymenoptera are $2n=92-94$ for the S.E. Asian ant *Platythyrea tricuspidata* Emery (Formicidae: Ponerinae: Platythyreini), and $2n=66$ for the North American paper wasp *Polistes exclamens* Viereck (Vespidae: Polistinae) (Hung et al., 1981). The *Platythyrea* count is corrected here by H.T.I. from the erroneous

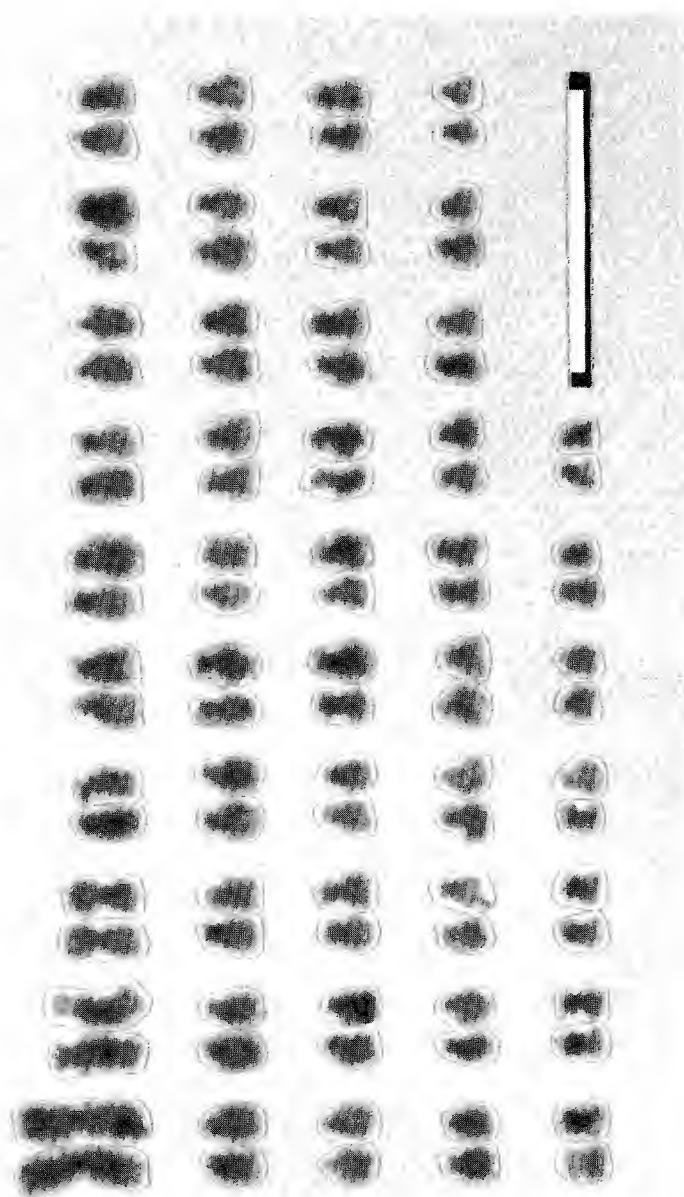


Fig. 1. Karyotype of *Nothomyrmecia macrops* $2n=94$ (scale = $10\mu\text{m}$).

original $2n=96$ of Imai, Brown et al., 1984 (the sole preparation has 2 cells with $2n=92$, 2 with $2n=94$).

N. macrops thus shares with *Platythyrea tricuspida* the highest chromosome number known for the order Hymenoptera.

The situation in *Myrmecia* Fabricius (subfamily Myrmeciinae), is even more interesting. *Myrmecia* is the genus considered most closely related to *Nothomyrmecia* (Taylor, 1978). It has a known range of chromosome numbers $2n=2$ to $2n=84$.

The $2n=2$ count is the lowest physically possible in a metazoan, and here unique to animals more advanced than the nematode *Parascaris univalens* (Goday and Pimpinelli, 1986). It is from an undescribed, chromosomally polymorphic, southeastern mainland Australian species first reported by Crosland and Crozier (1986), and referred to in our studies as *Myrmecia (pilosula) n=1*, which is known from detailed analysis to have $2n=2$, 3 or 4; $n=1$ or 2 (Imai and Taylor, 1989). It is a sibling relative of the "jack jumper" *Myrmecia pilosula* Smith, the nominate member of the *M. pilosula* species complex, which currently includes an estimated 6 morphologically closely similar but karyologically diverse putative species (with known chromosome counts of $2n=2-4$, 8, 9, 10, 15 and 17-32). All of these, except *M. pilosula* and one other, are taxonomically undescribed, and those previously represented in collections have generally been "lumped" under the name *pilosula*. One of them ($2n=8$, $n=4$) was discovered as recently as December 1989, in the vicinity of Denmark (34°58'S; 117°21'E), in extreme southern Western Australia, by H.T.I., M.K. and M.Y.W. Chromosomal details of another of these species, now believed nomenclaturally to be "true" *pilosula* ($2n=17-32$), were reported by Imai et al. (1988).

In addition *Myrmecia piliventris* Smith is known to have the chromosome complement $n=2$, $2n=4$, and to have closely similar relatives with much higher counts ($2n=6$, $n=3$ or 4; $2n=34$; $2n=64$ respectively; Imai and Taylor, 1986; Imai et al., 1988).

The highest *Myrmecia* count (that of *M. brevinoda* Forel, a large eastern "bull-dog ant"; Imai et al., 1988) is the next-highest after *Nothomyrmecia* and *Platythyrea tricuspida* in the Hymenoptera.

Thus, this single, morphologically compact genus of around 90 recognised Australian "morphospecies" (and one from New Caledonia) has a range of chromosome numbers almost as great as that known for its taxonomic order. Over one-third of the range of

chromosome numbers in the Hymenoptera is covered by the six *M. pilosula*—complex siblings alone, and almost two-thirds by the 4 species of the *M. piliventris* group studied to-date!

We therefore believe *Myrmecia* to be the most karyologically diverse of all animal genera, and the Formicidae one of the most diverse of all animal families.

Ninety species previously considered valid in *Myrmecia* were listed by Taylor (1987), with 150 available names, including putative junior synonyms, many of which are doubtless spurious. In our view there could be more than 200 biological species of the genus in nature, many of which are probably represented by specimens reclining cryptically in available collections under the names of putatively variable morphospecies, or as presumed junior synonyms. This estimate is based on the modest multiplication available names $\times 1.5$ ($150 \times 1.5 = 225$). This calculation would be a *radical underestimate* if the *pilosula*-complex statistics are at all representative of the genus at-large. They objectively justify a maximum multiplication factor of $6/2 = 3$ (6 currently known species *versus* 2 old available names), yielding an overall estimate of $150 \times 3 = 450$ *Myrmecia* species. In this light our estimate of 200 species is very conservative, but we consider it realistic. We expect, however, that the *pilosula* complex will prove to be more chromosomally diverse and species-rich than presently indicated, and this would have the effect of increasing the value of the maximum multiplier used above.

Myrmecia and *Nothomyrmecia* together encompass (1) the *whole* range of chromosome numbers known for the Hymenoptera; (2) much of the range known for the Class Insecta, where few counts higher than that of *Nothomyrmecia* are known (among the highest are several butterflies with counts up to $2n=446$, reported by White (1973 chap. 12)), and (3) a similar component of the known range for Phylum Arthropoda, where, for example, higher numbers than $2n=94$ were reported by White only from the previously mentioned butterflies, and a few decapod crustaceans (highest reported count $2n=376$).

Other ants with chromosome counts equalling or exceeding the vespid wasp maximum of $2n=66$ are *Myrmecia cephalotes* (Clark) ($2n=66$; Imai et al. 1977), *M. tepperi* Emery ($2n=70$; Browning 1987), and *M. pyriformis* Smith ($2n=81$; Imai et al. 1977); along with *Bothroponera rubiginosa* (Emery) (Ponerinae: Ponerini) ($2n=$

76; Imai, Baroni-Urbani et al. 1984), and *Monomorium latinode* Mayr (Myrmicinae: Solenopsidini) ($2n=70$; Imai, Baroni-Urbani et al. 1984).

A high chromosome number of $2n=92$, has been observed in the Mammalia, for the crab-eating water rat *Ichthyomys pitteri* (Gardner, 1971, Schmid et al., 1988). It is of some interest that both mammals and ants exhibit an extremely wide range of chromosome number variation: $2n=6-92$, and $2n=2-94$ respectively (for details see Imai, 1988; and Hoshiba et al., 1989).

The so called "fusion hypothesis" has long been invoked to explain the evolution of such variations in chromosome number (White, 1973). It suggests that chromosome numbers tend to reduce in evolution, mainly by centric fusion. An alternative model, the "minimum interaction hypothesis" was recently proposed by Imai, Maruyama et al. (1986). Here chromosome numbers as a whole are postulated to *increase* by centric fission (Robertsonian fission), thus minimizing the genetic risk resulting from reciprocal translocation, the occurrence of which is more likely between large chromosomes in low-numbered karyotypes ($n < 12$ in ants) than among small ones in high numbered karyotypes ($n > 12$ in ants) (Imai et al., 1988).

We stress that models of karyotype evolution must explain wide-ranging spectra of chromosome numbers among related organisms, like those demonstrated by mammals, or the Formicidae, or among the myrmeciine and nothomyrmeciine ants, including especially to date the *Myrmecia piliventris* and *M. pilosula* species complexes.

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SUMMARY

Chromosome numbers in the related Australian ant genera *Nothomyrmecia* and *Myrmecia* cover the whole range for the Order Hymenoptera (*Myrmecia* $2n=2-84$, *Nothomyrmecia* $2n=94$), and much of that for Phylum Arthropoda. Karyological statistics for

these and other ants are reviewed. *Myrmecia* appears to be the most karyologically diverse of all investigated animal genera, and the Formicidae one of the most diverse of all animal families.

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